



Instruments and Methods

Modelling the local distribution of cold-water corals in relation to bathymetric variables: Adding spatial context to deep-sea video data

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ABSTRACT

Video data and high-resolution multibeam bathymetry were acquired using a Remotely Operated Vehicle (ROV) on the flank of a carbonate mound (~850 m depth) in the Porcupine Seabight, SW Ireland. The ROV-mounted multibeam system revealed details of bathymetry that were not resolved by ship-borne multibeam survey, but appear to be important in structuring the distribution of the cold-water corals *Lophelia pertusa* and *Madrepora oculata*. Quantitative measures of slope, orientation, roughness and curvature were calculated from the ROV multibeam bathymetry data across a range of spatial scales. These parameters were analysed for their ecological relevance to the distribution of the corals and used in an Ecological Niche Factor Analysis (ENFA) to identify the most suitable areas for coral colonisation within the extent of our ROV multibeam data. The suitability map covers an area nine times the size of the area imaged directly by video. Cross-validation of the results with video data indicates that the predictions are reliable. This combined survey and modelling approach offers a comprehensive method for ground-truthing discrete seabed features such as mounds. It provides spatial context to high-resolution deep-water video observations and highlights the importance of bathymetric variables in influencing coral distribution.

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1. Introduction

Offshore mapping programmes such as the Irish National Seabed Survey (INSS) now commonly employ multibeam surveys to acquire bathymetry and acoustic backscatter data in deep water, beyond the continental shelf. The primary motivation for acquiring these data is often for broad-scale applications, including delimitation of national territories or hydrographic surveys. However, multibeam data have also proven invaluable for geological mapping (Todd et al., 1999), the mapping of general (Kostylev et al., 2001) and specific benthic habitats, e.g.,

cold-water corals (Fosså et al., 2005; Roberts et al., 2005) and can assist in the management of living resources (Kostylev et al., 2003). Besides revealing the general morphology of Ireland's offshore territory in unprecedented detail, the INSS multibeam survey (GOTECH, 2002) has identified many discrete morphological features, such as mounds, gullies and canyons. These represent anomalies in the general ecological gradients of the continental slope, and require targeted ground-truthing to determine their ecology and surficial geology.

On the Irish continental slope, some of the most prominent discrete features mapped to date are carbonate mounds. Recent evidence from shallow cores and deep drilled cores (IODP Expedition Scientists, 2005; Roberts et al., 2006; Rüggeberg et al., 2007) has shown that these mounds are built from successive periods of interglacial coral growth with intervening periods of glacial deposits. They range in size from less than 1 km to several km diameter (Fig. 1) and are of special ecological interest

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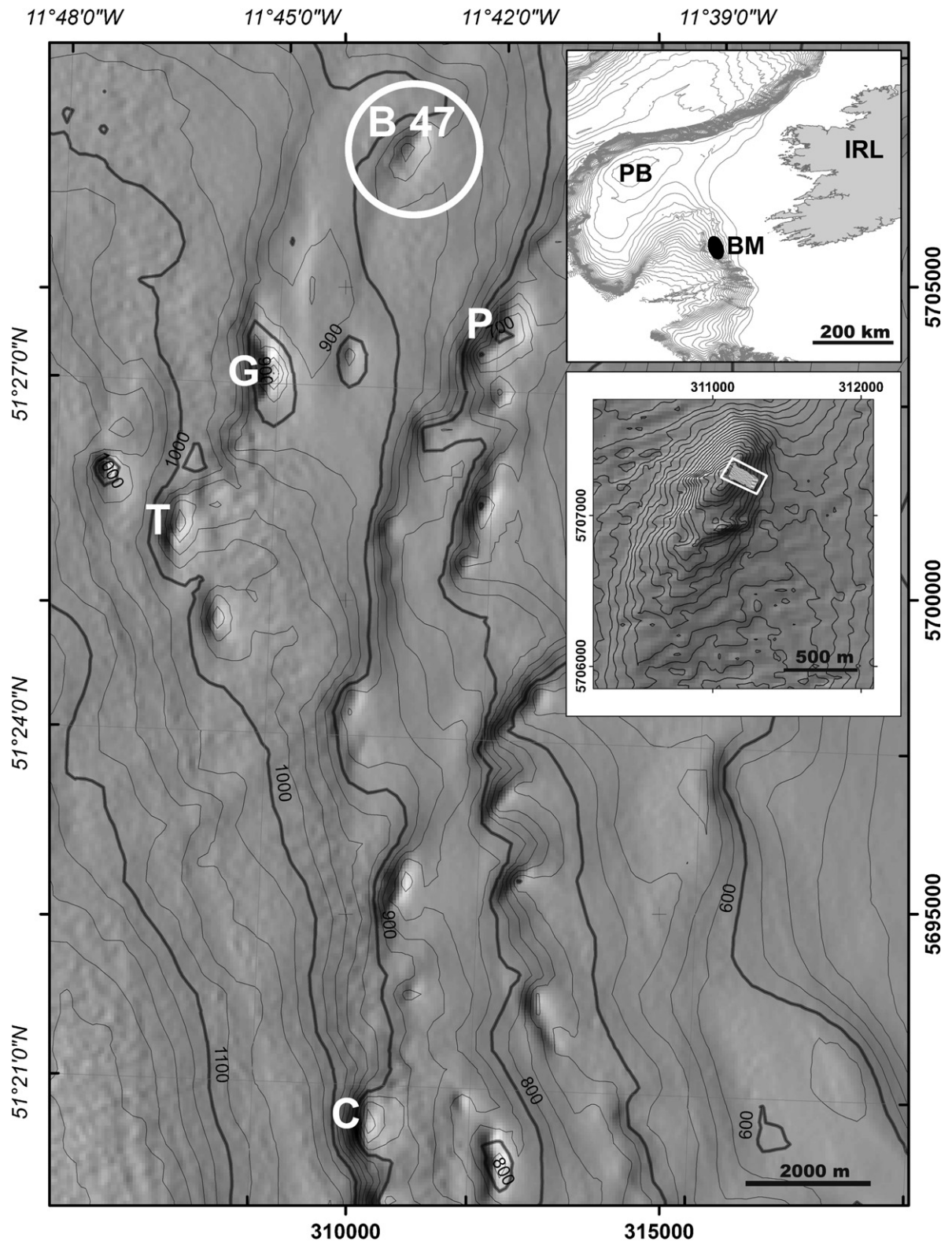


Fig. 1. The study area in the Belgica Mound province, Porcupine Seabight, SW Ireland. The position of the case-study mound BEL 47 (B 47) is shown in relation to some of the other better-known mounds in the province—Thérèse Mound (T), Galway Mound (G), Poseidon Mound (P), and Challenger Mound (C). Projected view (UTM Zone 29N (WGS84)) with geographic (WGS84) coordinates indicated for reference. Inset maps show the general location offshore Ireland (geographic view-WGS84) and the approximate location of the ROV dataset on BEL 47 (projected view UTM 29N, (WGS84)).

because of their frequent association with present-day cold-water coral communities (Wheeler et al., 2005a,b).

Discrete features such as carbonate mounds, occurring at mid-slope depths (700–1000 m), highlight a limitation of multibeam data acquired from a surface vessel in deep water, i.e., sounding resolution decreases with increasing water depth, because of multibeam geometry and the requirement to transmit at lower frequencies. So, whilst the general morphology and extent of such features is well mapped by ship-borne multibeam surveys (producing digital terrain models with a grid cell size typically 20–50 m), the local morphology and backscatter response of the mounds, which may be relevant to the ecology, are not resolved to the extent it would be in shallower water (digital terrain model grid cell size typically 0.5–10 m). This lack of fine-scale topographical context can make it challenging to interpret the results of any ground-truthing.

Traditional methods for exploratory ground-truthing of remote sensing information include physical sampling (grab, box-core, dredge). Video surveys are also becoming more common in the deep sea employing a variety of platforms with increasing levels of manoeuvrability and position fixing, i.e., towed video (Mortensen and Buhl-Mortensen, 2004), Remotely Operated Vehicles (ROVs; Grehan et al., 2005a; Foubert et al., 2005) and Autonomous Underwater Vehicles (AUVs; Clarke et al., 2006). Several surveys have also shown how high-resolution deep-tow sidescan sonar data may be effectively integrated with video data and/or sampling to produce local interpretations of the nature of the seabed (Huvenne et al., 2005; Wheeler et al., 2005a).

Each of these methods has limitation when used for targeted sampling of discrete features. For instance, to fully characterise the ecology and sedimentology of a mound many strategically located box-core samples would be required, which can be destructive, costly and time consuming in deep water. The footprint of such sampling devices ($<1\text{ m}^2$) is also small by comparison with the resolution of multibeam data at mid-slope depths (typically $>20\text{ m}$ grid cell size). Video surveys offer an effective, non-destructive means to provide a visual record of seabed surficial sediments and benthic megafauna over larger distances at a biologically useful scale. However, these data are constrained by the narrow field of view of the imagery (typically 1–10 m depending on camera/lighting configuration). In shallow water, where the field of view is similar to multibeam resolution, the structural and ecological changes observed in video data may be directly related to changes visible in multibeam data (Cutter et al., 2003). However, in deep water the synergy between ship-borne multibeam data and video observations is weakened by the differences in resolution. Combined video and deep-tow sidescan sonar surveys (Wheeler et al., 2005a) have highlighted the benefit of having an acoustic dataset, whose resolution is closer to that of the video observations. Sidescan sonar data, however, lack topographic information, which can be crucial in explaining variations in video observations and seabed acoustic response. Some swath acoustic systems (both beam-forming and interferometric) address this

limitation since they can provide both bathymetry and backscatter data.

High-resolution multibeam surveys, of resolution comparable to that of shallow-water surveys, have recently become possible in deep water ($>200\text{ m}$) with the development of a range of systems that may be mounted on underwater vehicles (Jerosch et al., 2007; Foubert et al., 2005). The quality of these multibeam data is improving through complementary advances in positioning and motion reference systems (Kinsey et al., 2006). Since multibeam surveys allow the concurrent acquisition of spatially coincident high-resolution bathymetry and backscatter data, they can be important in defining benthic habitat and serve as a complement to video data with the added benefit of a wider swath. Combined underwater surveys using both high-resolution multibeam and video surveys therefore offer an attractive prospect for rapid ground-truthing of discrete seabed features. As underwater vehicles become more widely available and more multibeam and video data are acquired in deep water, there is potential to develop methods that go beyond mapping of geology and ecology of the seabed, to provide a basis for predicting the distribution of fauna and benthic habitats.

In this study we present the results of one of a number of rapid reconnaissance surveys of carbonate mounds on the continental slope, SW Ireland, to illustrate how combining ROV-borne multibeam data with video enables prediction of the occurrence of benthic habitat beyond the extent of the video data. We demonstrate firstly how high-resolution data from a multibeam system mounted on an ROV can provide a spatial context for video data at comparable resolution. We then show how predictive models for the local distribution of cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) can be developed from video observations and high-resolution multibeam data.

L. pertusa and *M. oculata* have been associated with many previous studies on the Irish continental slope, (Bett et al., 2001; Klages et al., 2004; Olu-Le Roy et al., 2002; Wheeler et al., 2005b). Their distribution within the Belgica Mound province has been documented as part of sedimentary facies delineation (Foubert et al., 2005; Kozachenko, 2005; Wheeler et al., 2005a) and compared with the distribution in neighbouring areas (Huvenne et al., 2005). Studies of the relationship of corals to carbonate mounds (De Mol et al., 2002, 2007; IODP Expedition Scientists, 2005; Roberts et al., 2003) and past and present currents (Van Rooij et al., 2007; Van Rooij, 2004; White, 2006) have focussed on regional-scale patterns of distribution.

The factors affecting the distribution of cold-water (azooxanthellate) corals (Mortensen et al., 2001; Roberts et al., 2006; Thiem et al., 2006) include the availability of suitable substratum, favourable water-mass properties and the availability of food (often related to currents and seabed topography). Many of these are broad-scale ($>1\text{ km}$) parameters, but local-scale (10 cm–1 km) patterns of distribution, environmental gradients and links to topographic variables are also important to understand the spatial ecology of corals and habitat

structures at micro- to meso-scales (*sensu*; Greene et al., 1999). Without fuller understanding of their ecology and distribution, the management of corals and other benthic fauna will remain based on incomplete information and may not be adequate to protect from threats, e.g., fishing (Grehan et al., 2005a).

Despite the general focus of research on more regional patterns of mound and coral distribution several studies have indicated that there is local, intra-mound scale variability in the distribution of corals. A gradient in the distribution of corals between base and summit on several carbonate mounds (De Mol et al., 2007; Huvenne et al., 2005; Wheeler et al., 2005a) and seamounts (Genin et al., 1986) has been reported. One hypothesis to explain this is the variation in current speed, associated with acceleration over bathymetric highs, and its influence on food particle supply to the suspension-feeding corals. Local current effects are also thought to strongly influence coral distribution (Dorschel et al., 2007). ROV-based multibeam data on Thérèse Mound (Fig. 1) show that sediment waves up to 0.5–1.5 m high and with a wavelength of ~10–12 m persist across much of the mound (De Mol et al., 2007; Huvenne et al., 2005). Variations in coral cover associated with these sediment waves suggest that such local topography can have a significant effect on coral distribution.

Although the distribution of benthic fauna is controlled by a combination of environmental and biological factors, it is generally recognised that many animals show a particular affinity for certain types of terrain (Džeroski and Drumm, 2003; Roberts et al., 2003; Wilbur, 2000) which provide the physical habitat that is directly or indirectly suited to their mode of living. Bathymetry data and associated terrain properties, including slope, orientation, curvature and complexity (Wilson et al., 2007) are therefore important quantitative variables that can at least partially define the habitat that may be colonised by a certain animal. These parameters have the potential to act as predictor variables in models of the distribution of fauna, or habitat suitability (HS) models, and may be particularly valuable in the absence of other local-scale data.

This study explicitly examines the role of local bathymetric variables on coral distribution, through the use of a HS modelling technique, Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002). Using an example dataset from one particular carbonate mound, BEL 47, we demonstrate a ground-truthing methodology that can be used effectively and rapidly in conjunction with HS modelling to map discrete seabed features and benthic habitat for selected fauna in the deep sea. We focus on the following research questions:

- To what extent is a mound-scale environmental gradient important for the distribution of corals?
- In what ways does local topography on carbonate mound BEL 47 appear to affect the distribution of corals?
- How does HS modelling, and ENFA in particular, help quantify the relationship between coral distribution and local bathymetric variables?

- Which topographic variables have the most influence on coral distribution, and at what spatial scales?
- Does this quantitative approach offer significantly more ecological information than impressions gained from video data alone?

2. Methods

Our study utilises data from a survey conducted using an ROV on a carbonate mound in the Belgica Mound province, Porcupine Seabight, SW Ireland (Fig. 1). This mound is referred to as 'BEL 47' in previous literature (Crocker and O'Loughlin, 1998; De Mol, 2002; Wheeler et al., 2005a; Wilson, 2006) and was also nicknamed 'Erik Mound' after a video survey was conducted here by the Research Vessel 'Meteor' (Hebbeln et al., 2004). At a size of approximately 1 km by 500 m, and rising ~50 m above the surrounding seabed (810–860 m depth), BEL 47 is relatively small by comparison with others in the Belgica Mound province (Fig. 1). It was observed in multibeam surveys (GOTECH, 2002) conducted under the INSS and a survey reported by Beyer et al. (2003). We used the INSS multibeam data (supplied by the Geological Survey of Ireland), acquired using a Kongsberg Simrad EM120 multibeam (12 kHz), to produce a bathymetric grid of the mound at an optimum horizontal resolution of 25 m cell size. These data show the general morphology of the mound and provided essential background information for positioning the ROV-based survey.

BEL 47, like many carbonate mounds in the region, hosts cold-water corals, including the reef-forming species *L. pertusa* and *M. oculata*. Hebbeln et al. (2004) suggest that variability in the distribution of corals may exist over BEL 47, but existing video evidence is less extensive than for other Belgica mounds. As BEL 47 is also relatively small, it was a suitable target for ROV investigations during R.V. 'Celtic Explorer' cruise CE0505 in 2005. The ROV-based survey on BEL 47 was located between its base and summit in order to investigate the role of environmental gradients and local bathymetric variations in structuring the distribution of corals.

2.1. ROV-based data acquisition

ROV-based data were acquired in June 2005 during cruise number CE0505 (Grehan et al., 2005b) of the Irish National Research Vessel 'Celtic Explorer' using the 'Bathysaurus' ROV from Argus Remote Systems, Norway. A high-resolution Reson Seabat 8125 (455 kHz) multi-beam system, depth-rated to 1500 m, acquired co-registered bathymetry and backscatter data. The Seabat 8125 was mounted high on the front of the ROV and integrated with a sound velocity sensor. Data acquisition is possible at an altitude of ~100 m above the seabed with swath coverage approximately three to five times the altitude. The multibeam data presented here are from a single swath of data acquired when the ROV was flown at an altitude of 20 m from the summit to the base of the mound. These were the best quality data from a set of multi-altitude surveys conducted on this mound to test

the utility of single-swath surveys (Grehan et al., 2005b). The ship-borne data acquisition system was Reson PDS2000.

Positioning and attitude data were obtained using an IXSEA 'PHINS' photonic inertial navigation system. The PHINS unit was integrated with the ship's ultra-short baseline (USBL) system (IXSEA, 'GAPS') and aiding sensors (Doppler velocity log, depth sensor) to overcome drift during the dive. During operation, PHINS measurements are optimally merged using an internal Kalman filter (Napolitano et al., 2002) employing error models to provide the best position and attitude estimates in real time. Data from the PHINS were relayed to the PDS2000 data acquisition system for integration with the multi-beam data.

Video data were acquired using two colour cameras mounted on the ROV whilst flying at ~2 m altitude within the swath of the ROV-multibeam data. The primary mapping camera was a broadcast-quality Panasonic AWE-650 SDI, mounted to image the seabed vertically beneath the ROV. The focus and zoom of this camera were not varied in order that image size could be calculated (from the size of camera detector, lens focal length and altitude) and data were referenced using an internal time code preset from PDS2000. A second camera was mounted obliquely and imaged the seabed forward of the ROV. This camera provided qualitative images that could give context to the vertical observations. During data acquisition it served as a guide for piloting and obstacle avoidance. Good even lighting was achieved on each camera through the use of four high-intensity discharge lights and four halogen lights.

2.2. Data processing

Multibeam data were exported from PDS2000 and processing was conducted using CARIS HIPS/SIPS v.6.0. Sensor offsets, multibeam calibration values, navigation and attitude data were incorporated. Basic filters together with manual editing (e.g., to remove spurious depths) were employed to clean the bathymetric data. Backscatter data processing included slant-range corrections using the bathymetry and water sound velocity. Gridded bathymetry data were exported to GeoSoft Oasis Montaj, where they were further processed to remove any artefacts using directional cosine filtering (GeoSoft, 2005; Wilson, 2006). The fully processed bathymetry data were converted to raster grids for use in ArcGIS geographic information system (GIS). Backscatter mosaics were exported from CARIS as geo-referenced images.

Video data were integrated with navigation data using IFREMER's ADELIE software v1.7. This extracts geo-referenced video stills from the video stream. For the quantitative analysis we used video data sampled at 1-s intervals from the vertical video camera. This means that our species observations are geo-referenced directly beneath the ROV. We also examined co-registered oblique images, which give a wider view of the seabed ahead of the ROV. These provided more qualitative data and were helpful in providing context to the vertical observations and the multibeam data. We noted the presence of the

reef-forming cold-water corals *L. pertusa* and *M. oculata* within all vertical video images from a transect up the mound. Although these species do exhibit differences in their structure and form, these were not always discernable from the video images. For conservation purposes, both species are considered the reef-building component of 'coral habitat'; so we have not made any distinction between coral species in this pilot study.

All INSS and ROV-based bathymetry and video data were integrated in ArcGIS. The ADELIE extension for ArcGIS was used to provide a dynamic link to the video imagery and a user interface through which the presence of corals was noted.

2.3. Terrain analysis

Using the processed Seabat 8125 multibeam data, gridded at 0.5 m, we calculated quantitative descriptors of the terrain on BEL 47 at multiple scales. These descriptors included measures of slope, orientation, curvature and roughness, which cover the suite of variables that can be generated from bathymetry data (Wilson et al., 2007). All calculations were carried out in a GIS environment using ArcGIS (ArcInfo v8.3) and Landserf (Wood, 2005) software. Specific algorithms were employed for the computation of each parameter over a length scale defined by the number of cells in an $n \times n$ (where n is an odd integer) analysis window. We used a subset of the Fibonacci sequence (a mathematical sequence often occurring in nature, in which each number after the starting values 0, 1 is the sum of the two preceding numbers) to provide a template for progressively increasing window sizes. Where the sequence value was even, we adopted the nearest odd integer, giving $n = 3, 9, 17, 33$ (corresponding to ground distances of 1.5, 4.5, 8.5, 16.5 m) used in our analyses. Details of computation methods are provided by Wilson et al. (2007). An overview of the terrain analyses computed for the BEL 47 dataset is provided in Table 1.

Slope provides a quantitative measure of the rate of change in bathymetry over a particular length scale. Depending on the scale considered it may simply help define areas with sloping terrain that are favoured by corals (e.g., carbonate mounds), or it may offer a proxy to the availability of a suitable substrate for the corals (e.g., in relation to sedimentary processes). Slope may also offer an indirect measure of suitable positions in relation to currents, which vary in connection with slope (White, 2006) and supply food to the corals. *Orientation* (aspect) of the bathymetry is the direction of the steepest slope through a cell over the length scale considered. It provides a quantitative measure of the degree to which a specific location (cell) is exposed or sheltered from currents from a particular direction at a particular scale, and therefore may be important in determining the most suitable position for corals. Because a combination of current processes are always operating near the seabed at multiple scales in space and time, particularly on mounds (Dorschel et al., 2007), a suite of multi-scale variables describing orientation should be more likely to serve as successful predictors than orientation values at a single scale. Even so, orientation should only be considered a

Table 1

Terrain variables derived from ROV multibeam bathymetry data and used as environmental predictor variables in ENFA models

Parameter type	Parameter	Analysis window	Software
Slope Orientation (aspect)	Slope	$n = 3, 9, 17, 33$	Landserf 2.2 (Wood, 2005)
	Northness	$n = 3, 9, 17, 33$	Landserf 2.2 (converted to northness and eastness using ArcMap 8.3 Raster Calculator)
	Eastness		
Curvature	Bathymetric position index (BPI)	$r = 3, 9, 17, 33$	Based on methods described by Lundblad et al. (2006) but implemented without integer rounding in ArcMap 8.3 Raster Calculator
	Mean curvature	$n = 3, 9, 17, 33$	Landserf 2.2
	Profile curvature		
	Plan curvature		
Roughness	Fractal dimension	$n = 9, 17, 33$	Landserf 2.2
	Terrain ruggedness index (TRI)	$n = 3$	ArcMap 8.3 Macro provided by USGS (Valentine et al., 2004)
	Rugosity	$n = 3$	Jenness extension to ArcView 3.x (Jenness, 2002)

The size of the analysis windows used is given by values of n (Section 2.3). For BPI a circular analysis window is used with radius r .

general proxy variable that is connected somehow to these complex hydrodynamic processes. *Curvature* measures provide descriptors of the relative position of a particular cell in relation to its neighbours. For example, a cell lower than those surrounding it may form part of a trough (which may be either sheltered from currents or a pathway for them depending on orientation/size), whereas one that is higher than its neighbours may be a summit (which may be a point over which currents accelerate). Bathymetric highs, including carbonate mounds, are frequently associated with corals over scales of more than 10 m, suggesting that this property is particularly important on these spatial scales (Roberts et al., 2003). We have considered four measures of curvature (Table 1) in order to test whether this parameter is important at a local level (<10 m) and to determine which of these measures is most relevant to coral distribution. We have also computed three measures for *roughness* (our generic term for structural complexity) that have frequently been associated with marine and terrestrial biodiversity (e.g., Brown et al., 2002; Kostylev et al., 2005). The *fractal dimension* (Mandelbrot, 1983) was computed as a measure of structural complexity at several scales. For three-dimensional bathymetric data, the fractal dimension will vary between 2 and 3 (where 2 represents a flat seabed, and 3 represents a rugged, space-filling seabed) and this can be used in multi-scale benthic habitat analyses (Wilson et al., 2007). *Rugosity*, the ratio of surface area to planar area within analysis window, and *terrain ruggedness* (TRI), a measure of the local variability compared to central pixel of analysis window, were also computed at a single scale (Table 1).

Terrain variables are suited for use as indirect predictors of habitat for a certain fauna (Wilson et al., 2007). We appreciate that for a full description or model of suitable coral habitat, we should consider a suite of environmental factors that more completely define the habitat properties (e.g., currents, temperature, food availability, sediment distribution, etc.) in addition to

bathymetry and derived variables. Over small distances, however, where available data are not of sufficient resolution, we investigate the sole use of terrain parameters for the modelling of coral distribution.

2.4. Ecological Niche Factor Analysis

A variety of methods are available for multi-variate modelling of species distributions (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Segurado and Araújo, 2004); yet applications to the marine environment remain limited. The method of ENFA developed by Hirzel et al. (2002) is a HS modelling technique based on species presence data only. In contrast to some techniques (e.g., generalised linear models, generalised additive models; Hirzel et al., 2001; Guisan et al., 2002) it does not require absence data, which are difficult to obtain, costly or unreliable in the deep-sea environment.

Although its roots are in terrestrial ecology (Hirzel, 2001), ENFA has shown promising results in several recent marine applications. It was applied to model gorgonian coral distribution on a regional scale (Leverette and Metaxas, 2005; Bryan and Metaxas, 2007) using coarse environmental variables (Etnoyer and Morgan, 2007; Metaxas and Bryan, 2007). ENFA was also adopted to predict HS for stony corals on seamounts at a global scale (Clark et al., 2006) and in regional studies of cetacean distribution (Compton, 2004; Mandelberg, 2004). ENFA has been used to model squat lobster habitat using multi-scale terrain variables generated from ship-borne multibeam bathymetry data (Wilson et al., 2007). We are not aware of any previous studies that have used ENFA to model local-scale benthic habitat suitability, although the technique seems well suited to such application.

ENFA employs a suite of predictor variables, *Eco-Geographic Variables* (EGVs), for the study area and relates them to species observations in order to compute a HS model. In this study we used only terrain variables

(Table 1) as EGVs so our resulting model should be considered a partial HS or terrain suitability (TS) model. Particularly when applied on such a local scale we note that this is not ‘niche’ analysis in the full ecological sense (e.g., Pulliam, 2000). However, we use the term for consistency in connection with the method of Hirzel et al. (2002). For our ENFA analysis we used the freely available software BioMapper v3.1 (Hirzel et al., 2004). Details of ENFA theory are provided by Hirzel et al. (2002), and we outline the method below.

The EGVs are first reduced to a few uncorrelated factors using eigensystem computation. These factors explain most of the information related to the distributions of the original EGVs. They are not a subset of the EGVs in geographic space, but are new factors in EGV-space (Hirzel et al., 2002), which is the multivariate space in which the HS calculation is performed. The most important feature of ENFA (and that distinguishes it from principal components analysis) is that, rather than just accounting for the variance among factors, the ENFA factors have ecological relevance. The first factor accounts for all the *marginality* (M) of the species, i.e., how the occupied cells differ from the average conditions of the study area; this is related to the mean of the distribution. The other factors account for successive amounts of *specialisation* (S) that describe how selective the species is on the range of environmental conditions; this is related to the variance of the distribution. The contribution of individual EGVs to each factor gives an indication of their ecological relevance with respect to the species distribution. Unlike stepwise methods such as logistic regression, ENFA does not reject input EGVs (unless they are very highly correlated, in which case the correlation matrix will be singular, raising an error message in BioMapper); it merely weights them for importance on each factor (Hirzel et al., 2002). The amount of information explained by each factor in turn weights the EGV-space dimensions in which the HS is calculated based on the chosen algorithm. The theoretical basis for the various algorithms and their relative performance are discussed by Hirzel and Arlettaz (2004).

In this study, model performance was assessed using a k -fold cross-validation procedure based on the method of Boyce et al. (2002), which is implemented in BioMapper v3.1. This type of technique is well matched to the requirements of presence-only based models for which some more traditional evaluation techniques developed for presence-absence models are not applicable (Hirzel et al., 2006). The cross-validation method splits the species data into k sets and uses all but one of these to calibrate the model and the remaining set to validate it. Examination of the area-adjusted frequency (AAF) across the range of HS values provides a measure of model performance. AAFs are the frequencies of testing points lying within a bin, divided by the frequency of locations belonging to that bin across the study area (Hirzel and Arlettaz, 2004).

For a model with good predictive power the AAF should be <1 for unsuitable habitat and ≥ 1 (e.g., 10) for suitable habitat. For a poor model that predicts no better than by chance alone, AAF will be ~ 1 for all HS values. The

maximum value of AAF at the highest HS bin reflects the deviation from randomness (Hirzel et al., 2006) with higher values indicative of a better model. This value can be used to compare models for the same species within the same area and provides a means to test models produced using different algorithms and/or EGVs.

3. Results

3.1. Video

The video data, whilst of variable quality, are sufficient to obtain species presence records for the corals *L. pertusa* and *M. oculata*. Further analyses (e.g., presence/absence or estimates of cover density for certain species, qualitative descriptions of habitat class or coral health) are beyond the scope of this paper.

Visual examination of both vertical and oblique video data suggests that the corals tend to colonise the summits and southern sides of the observed sediment waves (Fig. 2). Using only the video data, however, this tendency can only be confirmed along the limited track of the video (~ 1 m wide), and it is difficult to get an impression of the spatial structure and organisation of the corals. Comparison of the video data with the pre-existing INSS bathymetry data (Fig. 3A) does not help to provide much information on the patterns of distribution of the corals since the resolution of the bathymetry (25 m grid) is too coarse. Although there are some variations in the occurrence of coral between the base and summit of the mound, no clear pattern is evident. We can merely see that coral occurs on this mound, possibly with a somewhat patchy distribution. This may be related to the few undulations we have seen on the video, but we have no means of making a quantitative link between these observations, or gaining further insight into the spatial context of the video observations using only the video and INSS data.

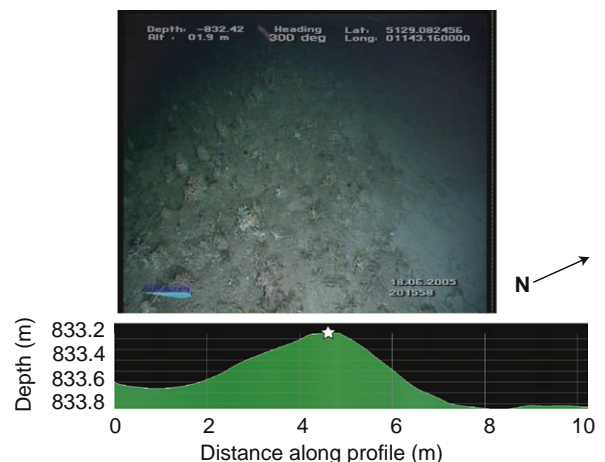


Fig. 2. Example of video imagery (oblique camera) showing coral distribution over a sediment wave on the flank of BEL 47.

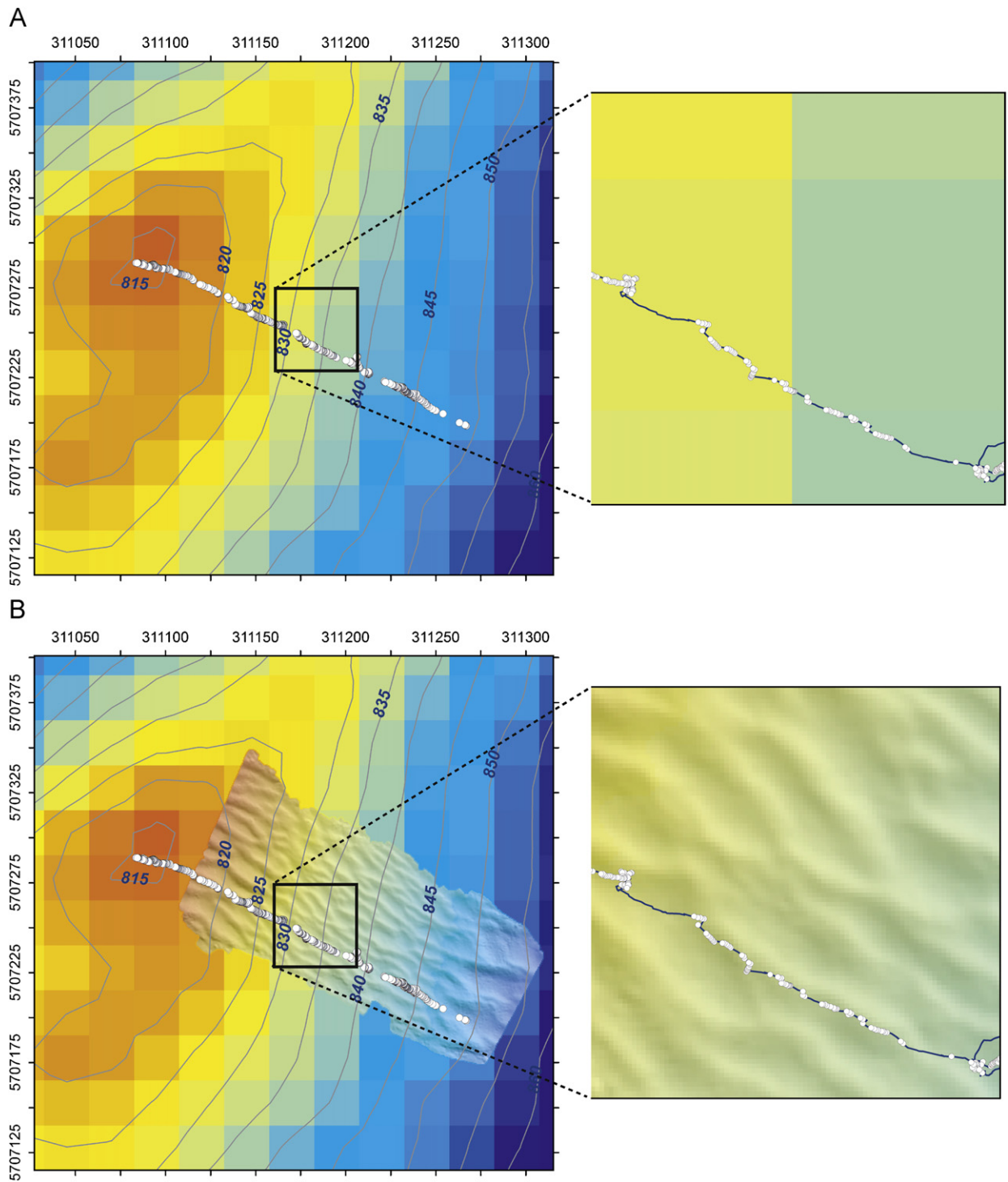


Fig. 3. Comparison of coral observations (white circles) from video data with (A) regional INSS ship-borne bathymetry data (25 m grid cell size) and (B) high-resolution ROV-based multibeam data (0.5 m grid cell size). Inset maps show close up views of a section of the data. Projected coordinates UTM Zone 29N (WGS84).

3.2. Multibeam

The 20 m ROV altitude used is suitable for detailed multibeam surveys, giving a good trade-off between

resolution and swath width, and generating data that can be gridded with a cell size (0.5 m) comparable to the extent of features observed in video imagery. The multibeam data within the single swath of data cover an area of

~90 m × 250 m. They reveal the presence of local-scale terrain variability in the form of persistent undulations across the flank of the mound. These appear similar to the sediment waves noted by previous authors on other mounds in the Belgica Mound province using sidescan (Wheeler et al., 2005a) and multibeam (Huvenne et al., 2005) data. Examination of the detailed ROV-based

bathymetry data together with our coral observations from the video data (Fig. 3B) shows that the data are suitable for investigating local topographic influences on the distribution of the corals.

Although backscatter data were also acquired during this survey, and show some evidence of variation in acoustic response associated with the sediment waves,

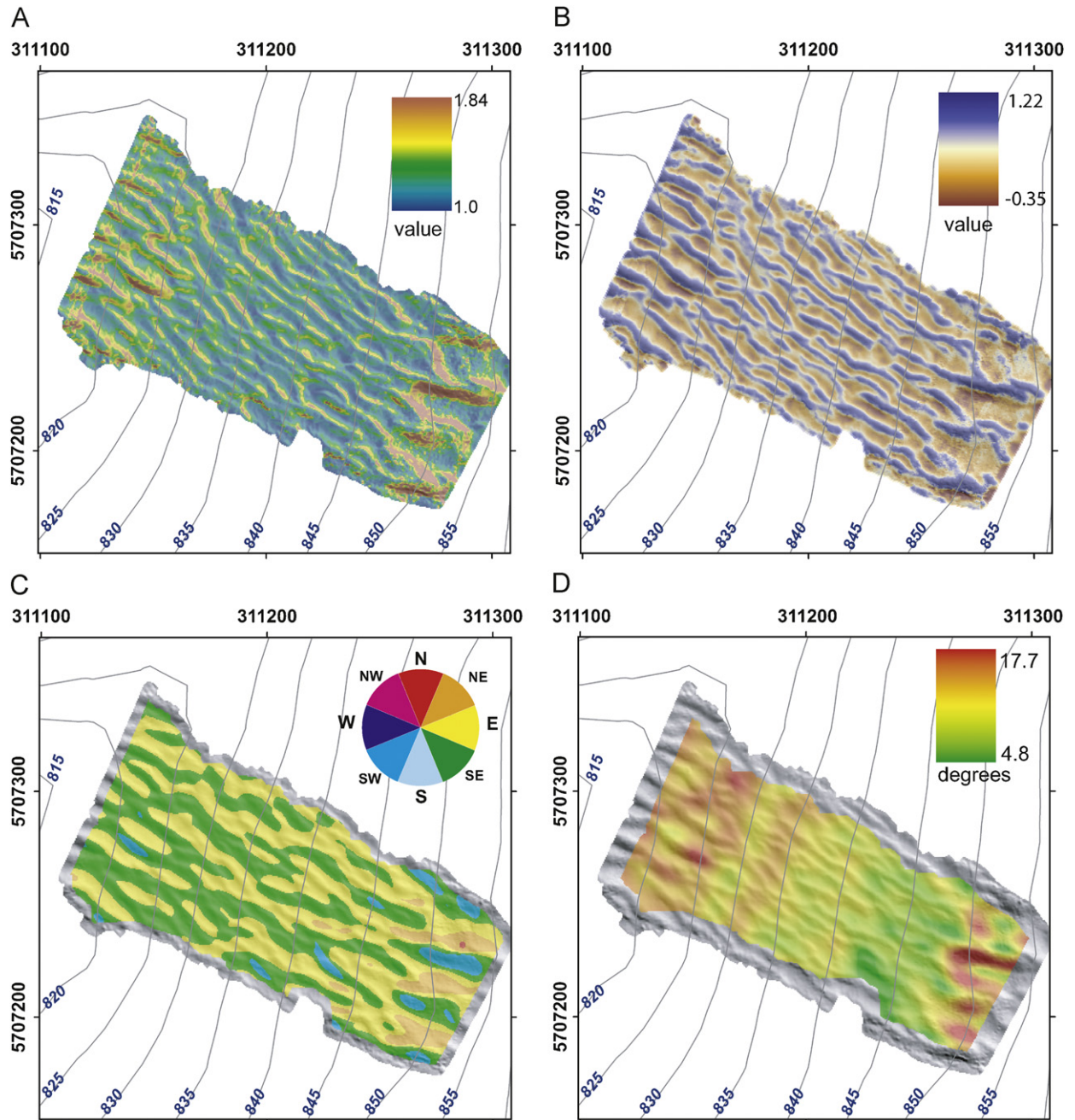


Fig. 4. Examples of terrain analysis from ROV-based bathymetry data (0.5 m grid). (A) Rugosity calculated using a 3×3 cell analysis window, (B) bathymetric position index (BPI) calculated using a circular analysis window of nine-cell radius, (C) aspect calculated using a 17×17 cell analysis window and (D) slope calculated using a 33×33 cell analysis window. Projected coordinates UTM Zone 29N (WGS84).

the nadir noise region is too dominant within this single swath of data for further use in quantitative analysis.

3.3. Terrain analysis

The terrain analysis (Table 1) successfully captures the topographic properties of the mound at different spatial scales. In Fig. 4, the various indices provide different information about the properties of the terrain, each of which may be relevant for the distribution of fauna (Figs. 4 and 5). The smaller-scale indices (Figs. 4A, B) capture variations associated with sediment waves, whilst the larger length scales capture the mound-scale properties, e.g., change in slope from base to summit (Fig. 4D).

In Fig. 5, aspect values are converted to eastness and northness indices for use in subsequent modelling. This is done to overcome difficulties associated with the 0–360° angle scale (i.e., 359° seen as distant from 0°; Wilson et al., 2007; Wilson, 2006).

3.4. HS modelling

All terrain variables (EGVs) listed in Table 1 were used as input predictor variables in the model. Following the covariance calculation, none of these EGVs were found to be too highly correlated to be retained in the model since all eigenvalues were positive (Hirzel et al., 2004), and the correlation trees in BioMapper showed satisfactory independence among variables. ENFA then reduced the EGVs to a set of uncorrelated factors in EGV-space. Seven factors were retained, based on a comparison with MacArthur's broken stick distribution (Hirzel et al., 2002; MacArthur, 1960). These explain 87% of the information (100% of the marginality and 74% of the specialisation) from the original variables. The relative contribution to each factor by the different terrain variables is indicated in Table 2 and the values give clues as to their ecological relevance.

Our results indicate that the corals colonise a limited range of terrain conditions within the multibeam swath. The first factor accounts for 100% of the marginality and 18% of the specialisation. Therefore, the parameters making the largest contributions to this factor are the key drivers for suitable coral habitat. These major contributors include the bathymetric position index (BPI; Lundblad et al., 2006), structural complexity (fractal dimension), and all measures of orientation. Examination of the sign of the values for the first factor indicates the preferred range of values on each parameter. We see that the corals prefer BPI values above the mean (i.e., positive features like ridges), and it seems the BPI is more relevant to the coral distribution than other measures of curvature. The corals prefer eastness values above the mean and northness values below the mean. In Fig. 5, a northness value below the mean corresponds to south-facing slopes, which at this local scale correspond to the southern sides of the sediment waves. The preference for high eastness values cannot be interpreted so literally. In fact the whole area is dominated by slopes with positive eastness values, (Fig. 5C) and there are hardly any west-facing regions.

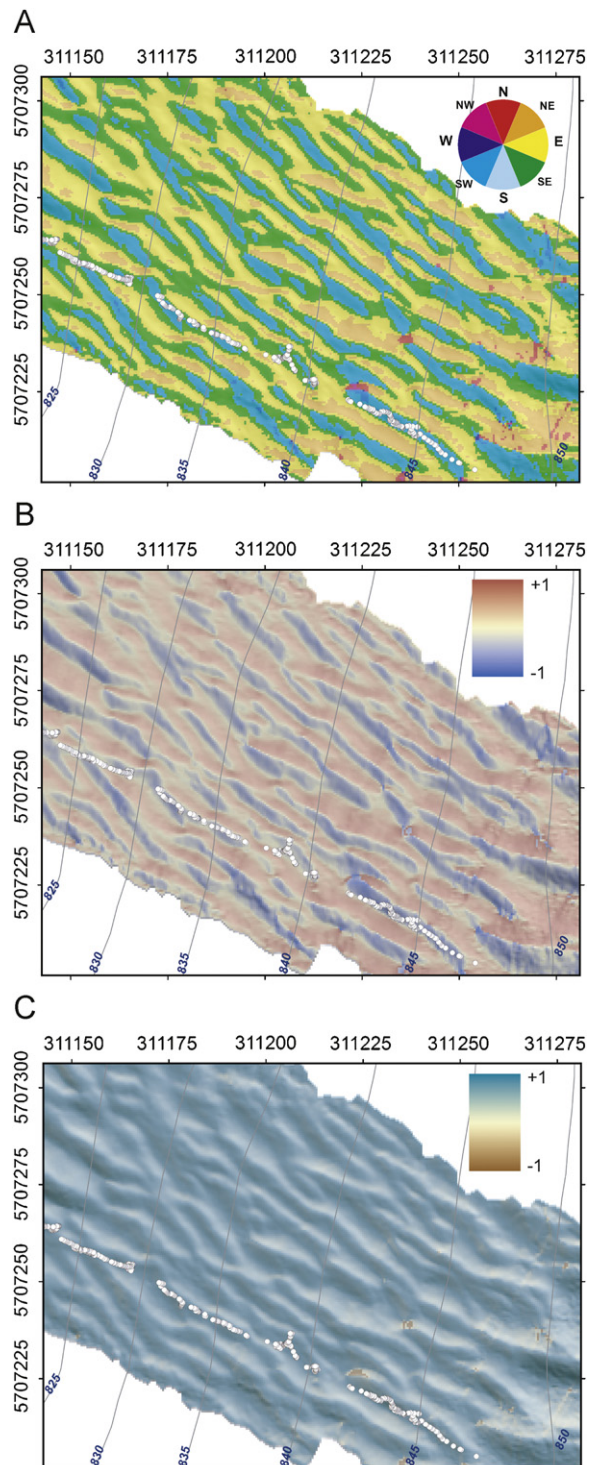


Fig. 5. Orientation calculations (3×3 cell analysis window) derived from ROV-bathymetry data (0.5m grid). (A) Aspect in degrees from north, (B) northness and (C) eastness. Projected coordinates UTM Zone 29N (WGS84).

Even at this most local scale, visually we observe little variation associated with the sediment waves. The fact that this parameter remains important in the model,

Table 2

Contribution of predictor variables to factors generated by ENFA

Predictor variable	Factor 1 <i>M</i> (100%), <i>S</i> (18%)	Factor 2 <i>S</i> (17%)	Factor 3 <i>S</i> (13%)	Factor 4 <i>S</i> (9%)	Factor 5 <i>S</i> (8%)	Factor 6 <i>S</i> (5%)	Factor 7 <i>S</i> (4%)
Bathymetry	0.112	−0.078	−0.263	0.091	−0.08	0.013	−0.088
BPI (3)	0.116	0.011	−0.008	0	−0.046	0.112	−0.06
BPI (9)	0.155	0.072	0.265	0.175	0.068	−0.363	−0.069
BPI (17)	0.126	−0.007	−0.287	0.138	0.11	0.179	0.322
BPI (33)	0.053	−0.14	−0.109	−0.056	−0.063	0.083	−0.128
East (3)	0.16	0.029	−0.066	−0.011	0.024	−0.161	0.23
East (9)	0.208	−0.059	0.054	−0.256	−0.108	0.309	−0.481
East (17)	0.314	0.2	0.067	0.244	0.213	−0.168	0.204
East (33)	0.173	−0.462	0.467	0.01	−0.009	−0.055	0.045
FD (9)	0.232	−0.001	0.002	0.093	0.005	−0.01	−0.035
FD (17)	0.041	0.034	0.033	0.055	−0.093	−0.006	−0.029
FD (33)	0.139	−0.013	0.001	−0.034	0.237	−0.047	−0.024
Mean curvature (3)	−0.014	−0.007	−0.012	0.034	−0.155	0.03	−0.243
Mean curvature (9)	−0.001	0.026	−0.035	−0.007	0.192	−0.192	−0.011
Mean curvature (17)	0.029	0.06	0.143	−0.277	−0.492	0.005	−0.058
Mean curvature (33)	−0.023	0.575	0.546	0.501	−0.215	0.106	0.27
North (3)	−0.477	−0.028	0.06	0.064	−0.088	0.243	−0.274
North (9)	−0.479	0.019	0.015	0.085	0.334	−0.393	0.151
North (17)	−0.364	0.012	−0.025	0.046	−0.219	0.203	0.253
North (33)	−0.095	−0.364	0.268	0.004	−0.052	−0.167	−0.157
Plan curvature (3)	−0.022	0.003	−0.011	0.073	−0.171	0.041	−0.256
Plan curvature (9)	−0.054	0.081	0.065	0.077	0.137	−0.275	−0.007
Plan curvature (17)	−0.024	−0.003	−0.025	−0.093	−0.185	0.021	0.034
Plan curvature (33)	0.045	0.408	0.235	0.5	−0.165	0.209	0.243
Profile curvature (3)	−0.046	0.021	0.015	0.002	0.118	−0.026	0.097
Profile curvature (9)	−0.118	0.001	−0.024	−0.033	0.005	0.124	0.06
Profile curvature (17)	−0.065	−0.015	−0.017	0.068	0.043	0.023	−0.028
Profile curvature (33)	0.004	−0.206	−0.159	−0.285	0.032	−0.099	−0.168
Rugosity (3)	−0.012	0.023	−0.073	0.004	−0.096	−0.075	0.023
Slope (3)	0.047	−0.007	0.01	−0.106	−0.035	−0.1	0.132
Slope (9)	0.013	−0.089	−0.124	−0.146	−0.007	0.332	0.018
Slope (17)	−0.088	0.124	0.126	0.211	−0.202	−0.229	0.05
Slope (33)	−0.148	−0.041	0.092	−0.152	0.333	−0.042	−0.108
TRI (3)	0.021	0.004	0.084	0.028	0.2	0.04	−0.108
Modelling summary							
Number of retained factors: 7							
Explained information: 87%							
Explained specialization: 74%							
Marginality (<i>M</i>): 1.009							
Specialisation (<i>S</i>): 3.447, Tolerance (1/ <i>S</i>): 0.29							

Those predictor variables making the largest contributions ($> \pm 0.1$) to the first factor are highlighted in bold. On the first factor, positive values indicate a preference for values above the mean value for a particular EGV, while negative values indicate a preference for values below the mean. On all other factors the signs have no ecological relevance. Numbers in parentheses denote the analysis scale used, *n*, or in the case of BPI, *r*.

however, suggests that small variations in eastness values are important, possibly because they are linked with shifts in the value of northness.

Fractal dimension values indicate a preference for more rugged terrain at local and broad scales, although other factors are more important at intermediate scales. This parameter seems more relevant than rugosity and TRI at delineating habitat for this dataset and is therefore either a better metric for complexity, or simply one that has been calculated at a more appropriate scale. Whilst most of the variables appear important at smaller spatial scales, we note that broader-scale slope makes an appreciable contribution to the first factor. This finding, together with the broader-scale influence of orientation and complexity, suggests that local-scale topography

associated with the sediment waves influences the coral distribution, along with some contribution from mound-scale influences.

In Table 2 the absolute value for each predictor variable on the all but the first factor reflects the degree of specialisation on that variable. Good models were obtained with both the harmonic mean and minimal distance algorithms (Hirzel and Arlettaz, 2004), and both indicate that the most suitable habitat is found on the wave crests and preferentially towards the SW sides of these waves. Results produced with the harmonic mean algorithm are shown in Fig. 6. Cross-validation using 10 sets (Fig. 7) confirms that our model is well fitted. For low HS values we obtain mean AAF values well below the random frequency line. These increase

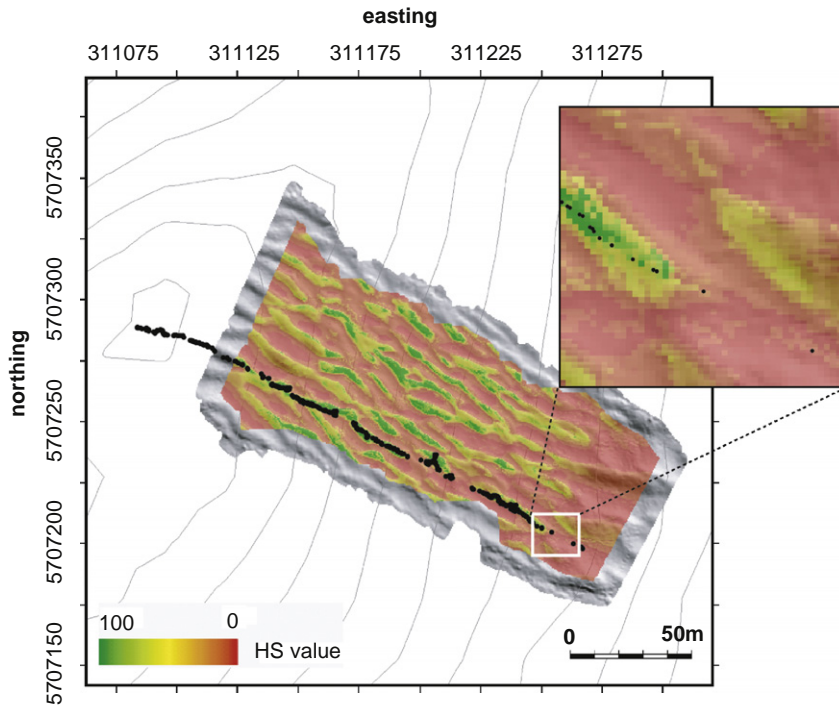


Fig. 6. Predicted habitat suitability for cold-water corals *Lophelia pertusa* and *Madrepora oculata* on BEL 47 within the region covered by ROV multibeam survey at 20 m altitude. Habitat suitability map generated using ENFA using the harmonic mean algorithm and seven retained factors. High habitat suitability values (green) indicate areas with the most suitable habitat for corals, decreasing to the least suitable habitat (red). Inset map shows how coral observations (black dots) mainly fall within pixels with a high habitat suitability score. A few observations are encountered in pixels with moderate-low scores reflecting the fact that corals may not always occur in optimal habitat. Projected coordinates UTM Zone 29N (WGS84).

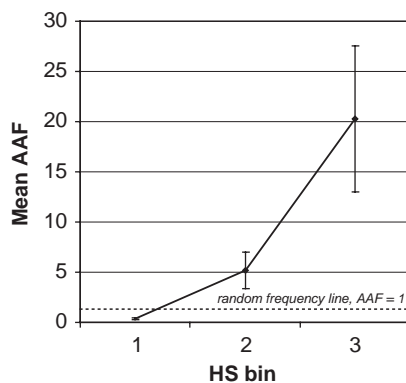


Fig. 7. Cross-validation results for habitat (terrain) suitability model (Fig. 6) for cold-water corals on BEL 47. Model produced using ENFA, harmonic mean algorithm. Mean area adjusted frequency (AAF) indicates the number of species occurrence records encountered between runs of the k-fold cross validation, using $k = 10$. Error bars show the standard deviation. Values are shown for three habitat suitability bins ranging from low HS scores (bin 1—unsuitable habitat, HS values 0–33) through to high HS scores (bin 3—most suitable habitat, HS values 66–100). These three bins correspond to the level of sensitivity that can be expected from our model, although other values could be used in reclassification.

monotonically for higher HS values, consistent with the requirements for a good model described by Hirzel et al. (2004).

4. Discussion

4.1. Mound-scale gradients

Corals were present along the video transect from the base to the top of the mound within the area bounded by the multibeam data. Additional video observations acquired during the same transect but beyond the extent of the multibeam data (and therefore our model) indicate that corals persist to the summit of the mound. Coral presence (observed and modelled) appears sparser in the lower portion of the mound, but our results are inconclusive as to whether this is due to mound-scale effects, local topographic effects or merely patchiness in recruitment success. This study is only concerned with coral presence, not abundance, but we did also note qualitatively from the video data that there are variations in the density of coral cover along the transect. The corals appear more frequently towards the top of the mound, slightly below the summit. This is consistent with observations by other authors on nearby mounds (De Mol et al., 2007; Foubert et al., 2005; Huvenne et al., 2005; Wheeler et al., 2005a). This suggests that mound-scale controls related to the depth (or distance from summit) are important in determining *optimal* habitat conditions and hence abundance, but not so dominant that they restrict the presence of corals, which persist at all depths on this mound.

4.2. Local topography

Even from the video data alone (Fig. 3) we can see that the distribution of corals is related to the local topography. Visual assessment, terrain analysis and modelling from BEL 47 (Section 4.4) suggest that the corals respond to local roughness (i.e., the sediment waves) and seek out local topographic highs. This is consistent with observations by Huvenne et al. (2005) on nearby Thérèse Mound.

Additional multibeam data from higher altitudes were also acquired over a wider area of the mound during the same dive, but because of its variable quality, it was not suitable for use in construction of our model. These data did confirm, however, that the sediment waves extend across the entire mound and are not restricted to the side of the mound illustrated in this study. The orientation of the ridge crests remains roughly perpendicular to the contours on each side of the mound.

4.3. Ecological Niche Factor Analysis

The quantitative terrain descriptors (EGVs) serve as effective predictor variables for the distribution of suitable local habitat for the corals. The relative importance of these EGVs to the various factors in ENFA (Table 2) can be used to assess their relative contribution to defining areas of suitable habitat. The model developed using ENFA is successful at discriminating between suitable and unsuitable habitat across the flank of the mound, within the swath of the multibeam data, and cross-validation results confirm that the model is well fitted. The results presented in Fig. 6 show a full range of values from 0 to 100. However, the model is probably more suitable for classification to more general classes (e.g., suitable, moderately suitable and unsuitable terrain/habitat) since the continuous scale can imply an unrealistic sensitivity to HS (Hirzel et al., 2006).

The ENFA technique appears well matched to available data and modelling requirements. Presence-only techniques such as ENFA seem well suited to use with deep-sea video data, which may encounter difficulties generating adequate data (e.g., presence-absence, abundance) required for other modelling techniques. Although it is not designed for abundance modelling, it is possible to modify the ENFA to use weighted species observations, reflecting the abundance, in construction of the model. Since our video frames were of roughly the same dimensions as the EGV cells and often contained only one coral colony, this was not attempted in this initial study.

4.4. Topographic predictor variables

Our model can discriminate between suitable and unsuitable habitat and clearly predicts that areas of most suitable terrain are found on the SW-facing edges of the sediment ridges. This is consistent with the direction of the predominant current (White, 2006) in the study area and implies that the corals benefit from an improved food supply by locating on the leading edge of these local topographic highs. The parameters

having greatest influence on our model are dominated by those that most effectively capture these ridges, at small to intermediate scales. These include the BPI, orientation and structural complexity. Broad-scale slope and complexity are also important, suggesting that there are also other influences over longer length scales closer to the mound-scale.

Through detailed bottom current measurements over a mound not far from our study site, Dorschel et al. (2007) have shown that there is a complex interplay of current processes at work on several spatial and temporal scales. Coral cover is linked to locally enhanced bottom currents. However, they are also influenced on broader scales by contour currents, tidal currents and topography, which also influence sedimentation and food supply. Our topographic model can only hope to provide proxies to some of these important processes.

The specific results of our topography-based model may only be relevant to this study site, but the ENFA technique employing topographic predictor variables seems suitable for wider application. Particularly in light of our limited video observations our model is unlikely to rule out chance events and patchiness in recruitment success, which may mean the corals are not just located in the most suitable terrain. Nevertheless the approach seems valid as long as we are mindful of the model limitations. The ENFA approach does not claim that no corals will occur in 'unsuitable' habitat, just that they are less likely to do so than in 'suitable areas'.

4.5. Comparison of combined, quantitative approach and video survey only

Our approach gives a quantitative prediction of the relative suitability of all cells within the area covered by the multibeam data, not just a qualitative interpretation of their likely distribution based on the limited extent of video imagery. This combined survey method, together with modelling, offers a valuable complement to video surveys, which lack spatial or structural context.

Our model is of course only a terrain suitability model, but this appears to be an effective delineator for habitat, particularly where the coral distribution responds to local topography. Even using this limited range of predictor variables we gain new insights into coral distribution, and structural organisation that would not be possible using video observations alone. We have effectively ground-truthed this flank of the mound and the predicted habitat map covers an area around nine times greater than the area imaged directly by video. Since it will never be practical to perform 100% video mapping this approach offers a practical alternative to video surveys alone for examination of local habitat. This type of modelling would not be successful if there is no local variation in terrain, or if the target fauna do not respond to changes in terrain. However, ENFA is suited for employing other types of quantitative and semi-quantitative data (Hirzel et al., 2002), e.g., bottom current velocity and interpreted sediment distribution maps, if such data become available.

4.6. Survey implications

The combined ROV-based survey approach is well suited for benthic habitat mapping in the deep ocean, particularly for ground-truthing discrete seabed features. The ROV multibeam data should be acquired first during the dive in order that the habitat structure can be elucidated in advance of the video survey. The precise video transect can then be planned to cover features identified by the multibeam data. Regularly spaced species surveys are recommended by Hirzel and Guisan (2002) as a basis for HS modelling. Whilst such survey designs are difficult given the practical constraints of deep-sea surveying, we note that a better model might have been obtained if our video data coverage was equally spaced across the swath and among crests and troughs of the sediment waves, rather than along the single base-summit transect, which generally followed the orientation of the crests/troughs. Our model appears to perform adequately despite this limitation in the input data. However, we acknowledge that predictions are made on a limited dataset. A zig-zag video transect from mound base to summit would generate a more comprehensive dataset to allow cross-mound variations in habitat structure and faunal colonisation to be directly sampled with the video. Such a survey should be feasible with an ROV similar to the one used in this study, although the tether to the surface vessel inherent to ROV systems requires coordinated movements between ship and ROV which can be challenging, particularly in poor sea conditions. More extensive surveys, including more complex survey patterns, may become easier to undertake through the use of AUVs. Movements of AUVs are not restricted by a tether, and if supported by suitable navigation and control systems (e.g., Molnar et al., 2005) they can operate safely near the seabed to acquire multibeam and video data.

Production of HS maps will be improved if high-quality multibeam backscatter data can be collected and suitably processed, as these provide a (semi-) independent dataset, which can act as a proxy for seabed surficial sediments (e.g., Dartnell and Gardner, 2004). Whilst little variation may be expected at a local level on other oceanographic drivers for benthic habitat (e.g., temperature), some parameters could provide very useful information (e.g., local bottom current velocity, turbidity) that would allow modelling to move beyond TS modelling to a fuller environmental habitat model for the target fauna. A survey reported by Grasmuseck et al. (2006) illustrates how such a dataset can now be acquired using an AUV platform, although the video observations were performed separately in this study. Nested surveys incorporating several technologies that help bridge the scale gap between local and regional information clearly generate fuller datasets for modelling and may incorporate alternative technologies to bridge the scale-gap, e.g., laser line-scan rather than multibeam (MacDonald et al., 2003). However, such comprehensive datasets are expensive and require coordinated research efforts over a period of time. We have shown that much information can be obtained using a rapid and relatively simple survey to ground-truth

a discrete feature such as a carbonate mound, particularly when the results are combined with habitat modelling techniques like ENFA.

5. Conclusion

This case study demonstrates that sub-mound scale bathymetry has an influence on the local distribution of corals. Variations in local bathymetry, resolved by ROV-based multibeam bathymetry data across the flank of BEL 47, were used to generate quantitative descriptors of the terrain at multiple scales. These terrain variables were used in a multivariate statistical model that determines the most suitable areas for the occurrence of reef-forming cold-water corals on a local basis. Those variables with the most influence on coral distribution within our area are bathymetric position, orientation and structural complexity, each at scales that most effectively capture the sediment waves that persist across the flank of this mound. It is likely that these parameters define the corals' most favourable position in relation to currents associated with the supply of food.

Increasing our understanding of the local spatial organisation of coral communities in relation to bathymetric variables may enable a more effective utilisation of ship-borne multibeam data for HS prediction at regional scales. In the deep sea, where opportunities for sampling and surveying remain limited, the application of predictive modelling techniques that improve the robustness of extrapolated habitat distribution maps for corals and other megafauna offers a cost-effective means of providing this vital information to resource managers.

The approach presented here maximises the information gathered in one survey and provides an effective method for ground-truthing discrete seabed features, bridging the resolution gap in the deep sea between ground-truth data and ship-borne multibeam data. The acquisition of accurate geo-referenced high-resolution multibeam and video data greatly enhances our understanding of bio-geological interactions and provides quantitative data crucial for the development of HS models. The ENFA habitat (terrain) suitability modelling technique has been shown to be effective in predicting the extent of coral cover beyond the track of the video data. Similar modelling techniques have the potential to quantify suitable habitat for other deep-sea fauna both at local and on broader scales, through incorporation of additional predictor variables.

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